VARIATIONS IN THE BLOOD CHEMISTRY OF
THE LOGGERHEAD SEA TURTLE, *CARETTA CARETTA*

PETER L. LUTZ AND ANN DUNBAR-COOPER[1]

ABSTRACT

The natural blood chemistry profile of loggerhead sea turtles living in Cape Canaveral waters was determined over a 3-year period. Overall plasma osmotic pressure, potassium, and magnesium values were similar to those reported for other reptiles, sodium and chloride was much less than for sea snakes. Plasma calcium and glucose values were among the lowest of any reptile. Osmotic pressure, sodium, and potassium values increased during the warmer months. Chloride and in particular magnesium, glucose, and hematocrit levels were comparatively constant. Calcium and urea values showed wide variations but no seasonal trend was apparent. Changes in urea concentrations closely tracked those of osmotic pressure. Blood lactate values from trawl-captured sea turtles were 10-80 times higher than those from quiescent sea turtles and calculations suggest that at least 20 hours is required for full recovery. The complex changes in blood chemistry observed reflect changes in the sea turtle physiology and biochemistry; significant changes from normal in plasma magnesium, potassium, and hematocrit could be useful indicators of hibernation in sea turtles.

For any animal a knowledge of the normal pattern and changes in blood chemistry can be related to its physiological state and can also be used to identify chronic and pathological conditions. With the exception of sea turtles, there are many studies and reviews on seasonal changes in the blood chemistry of reptiles (Dessauer 1970; Duguy 1970; Gilles-Baillien 1974; Minnich 1982). Since there is an urgent need to understand the ecological physiology of these endangered and threatened species, this lack of information on sea turtles is undoubtedly due to the logistical difficulties of long-term sampling of a wild marine population.

The year-round presence of large numbers of loggerhead sea turtles, *Caretta caretta*, in and around the Port Canaveral ship channel provided a rare opportunity to study the monthly changes that occur in the biology of this little understood group of animals. Such a study was rendered all the more urgent by finding, in the winter of 1978, numerous black stained and apparently torpid turtles lodged in the mud of the ship channel (Carr et al. 1980). It was suggested that the loggerhead sea turtle was able to survive prolonged exposure to cold seawater temperatures (less than 15°C) by partially lodging in the mud at the bottom of the Port Canaveral ship channel and by going into a state of winter dormancy or apparent hibernation (Carr et al. 1980; Ogren and McVea 1982). If this hypothe-

sis were correct, it would mean that the Cape Canaveral ship channel was serving as a hibernaculum for this endangered species and the identification of features that could confirm hibernation in these loggerhead sea turtles was of some practical importance. For this purpose, a study of blood chemistry is particularly apt. There is abundant evidence of significant changes in certain blood constituents in hibernating mammals (Fisher and Manery 1967; Soivio and Kristoffersson 1974; Al-Badry and Taha 1983) and there are a few studies showing similar changes in some reptiles (e.g., freshwater turtles, Hutton and Goodnight 1957; lizards, Haggag et al. 1965).

The purpose of this study was to establish the normal seasonal changes in blood chemistry that occur throughout the year in the Cape Canaveral population of loggerhead sea turtles and from this base of data to identify, if found, those animals that are in a state of hibernation.

METHODS

Selected National Marine Fisheries Service (NMFS) shrimp trawl turtle surveys of the Port Canaveral ship channel were accompanied by the authors from December 1978 to August 1982. On board ship the activity levels of newly caught loggerhead sea turtles were observed, and body temperature, weight, and sex recorded. Blood samples were taken from freshly captured sea turtles, using a heparinised syringe, from a venous sinus on the

[1]Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149.

lateral dorsal region of the neck (Bentley and Dunbar-Cooper 1980). Some sea turtles were also resampled after 3, 4, and 5 h on deck. The hematocrit was measured on board ship immediately after taking the sample. Blood cells were centrifuged and plasma stored on ice for transport to Miami. The plasma was frozen until used ($-4°C$).

The items that were measured are as follows: Plasma osmotic pressure, using a Wescor vapor pressure osmometer; sodium and potassium concentrations, by flame emission spectrophotometry; calcium and magnesium, by atomic absorption spectrophotometry using appropriate standards (Lutz 1972); chloride, using an Aminco Chloridometer; and urea and glucose, using enzymatic kit techniques (Sigma).

The blood chemistry values reported are means ± SD. Statistical differences between groups were determined with Student's t test, and level of significance was set at $P < 0.05$ for all comparisons.

RESULTS

Hematocrit

The hematocrit levels of the loggerhead sea turtle were remarkably constant and were not influenced by season (Table 1). The range of values was 28-48%, and the mean 35.4% is very similar to that found by Dessauer (1970) for the same species (32%). The sea turtles caught in December 1978 were a striking exception to this uniformity with very much lower mean hematocrits (15%) and one individual having a value as low as 5%.

Loggerhead sea turtles resampled 3-5 h after capture showed some interesting changes. Four animals resampled after 3 h on deck showed an average increase in hematocrit of 10.4% (±14.89), for five animals after 4 h the average increase was 4.8% (±4.7), and for four animals after 5 h the hematocrit had decreased on average 15.2 (±13.3) from the initial value. The reason for this change is not clear.

TABLE 1.—Blood chemistry values of loggerhead sea turtles trapped by shrimp trawl in the Port Canaveral of samples in parentheses. Groups that differ significantly

Date	°C	Na	K	Ca	Mg	Cl
Dec. 1979	21.0	150.2 ± 13.45 (5)	3.7 ± 0.81 (4)	1.09 ± 0.50 (5)	*1.7 ± 0.46 (5)	109.3 ± 11.36 (4)
Jan. 1980	18.0	138.1 ± 13.07 (11)	3.3 ± 0.49 (11)	1.4 ± 0.48 (13)	2.19 ± 0.30 (13)	105.9 ± 8.40 (11)
Feb. 1980	16.0	129.2 ± 12.7 (8)	3.05 ± 0.63 (8)	1.18 ± 0.86 (8)	1.84 ± 0.46 (8)	110.5 ± 11.71 (8)
Mar. 1980	18.0	142.2 ± 8.95 (6)	3.32 ± 0.63 (6)	1.04 ± 0.38 (7)	2.2 ± 0.56 (7)	108.6 ± 4.36 (5)
Apr. 1980	19.0	140.9 ± 4.7 (4)	3.58 ± 0.37 (4)	1.03 ± 0.16 (4)	2.24 ± 0.42 (4)	112 ± 10.42 (4)
May 1980	23.0	139.3	3.5	—	—	112
June 1980	24.0	139.5 ± 5.87 (6)	3.5 ± 0.40 (6)	0.86 ± 0.50 (5)	2.29 ± 0.41 (5)	103.5 ± 9.02 (5)
July 1980	25.0	143.1 ± 5.55 (7)	3.9 ± 0.83 (7)	1.08 ± 0.77 (7)	2.38 ± 0.39 (7)	*114.4 ± 3.34 (7)
Aug. 1980	28.0	139.5	—	1.58	1.75	121
Sept. 1980	—	145.2 ± 10.95 (5)	3.8 ± 0.65 (5)	1.4 ± 0.3 (5)	2.23 ± 0.46 (5)	**121.8 ± 16.4 (7)
Nov. 1981	24.0	**162.2 ± 7.93 (5)	**4.18 ± 1.49 (5)	**2.18 ± 0.325 (9)	1.49 ± 0.77 (5)	107.0 ± 3.25 (9)
Feb. 1982	19.0	142.07 ± 21.42 (4)	4.145 ± 0.69 (4)	1.863 ± 0.456 (5)	1.976 ± 0.303 (5)	102.7 ± 10.58 (10)
Mar. 1982	18.0	152.1 ± 14.2 (5)	**4.17 ± 0.454 (5)	1.40 ± 0.765 (10)	2.31 ± 0.66 (5)	108.86 ± 9.88 (10)
May 1982	24.5	*165.5 ± 4.41 (3)	*4.08 ± 2.04 (3)	2.09 ± 0.41 (8)	2.00 ± 0.62 (4)	110.3 ± 5.62 (9)
June 1982	27.0	**168.9 ± 4.09 (3)	**4.6 ± 0.48 (3)	1.78 ± 0.93 (10)	1.93 ± 0.55 (5)	108.2 ± 13.0 (9)
Aug. 1982	—	*159.3 ± 15.4 (5)	5.14 ± 0.83 (5)	1.69 ± 0.96 (8)	2.65 ± 0.69 (5)	**117.3 ± 6.57 (9)

It is too short a time lapse for an erythropoesis response particularly as sea turtle red cells can have life spans of 600-800 d (Altman and Brace 1962); but it is possible that the loggerhead sea turtle has a considerable ability to store and release blood cells on demand.

Sodium

Plasma sodium increased as the year advanced with minimal values found in February of each year followed by a gradual rise to maximums in late summer and early fall (Table 1). However, the range of values is very wide (Table 1); the lowest for an individual was 105.5 mM, the highest 173.0 mM. The mean sodium concentration for the whole population was 145.03 ± 13.80 mM (n = 82).

Chloride

Like sodium the highest values were found in the fall (Table 1), but the individual range, 102.7-131.2 mM, was much narrower than that found for sodium. The narrow excursion suggests that chloride is under comparatively tight control. The population average, 107.2 ± 18.80 mM (n = 86) is very similar to that reported by Dessauer (1970) (110 mM).

Potassium

The field data showed little change in the absolute potassium levels (Table 1). The population mean 3.82 ± 0.764 mM (n = 70) is considerably lower than that found for salt water adapted Malaclemys (8.8 mM, Dunson 1970). Minimal values were found in early spring (February) and a gradual rise was seen as summer advanced.

Calcium

Calcium values ranged quite widely over the sampling period and the results are fairly scattered and

ship channel, December 1979 - August 1982. Unless otherwise stated, units are mM. Mean ± SD, number from January 1980 group (* $P < 0.05$; ** $P < 0.01$).

Date	°C	Lactate	Glucose	Urea	Osmotic pressure mOsm	Hematocrit %
Dec. 1979	21.0	—	—	10.9 ± 6.64 (5)	315.2 ± 15.2 (5)	**15.67 ± 8.10 (4)
Jan. 1980	18.0	—	—	6.19 ± 2.82 (11)	301.5 ± 22.6 (11)	34.9 ± 2.70 (9)
Feb. 1980	16.0	—	—	4.56 ± 1.86 (8)	300.4 ± 20.6 (7)	36.1 ± 7.18 (7)
Mar. 1980	18.0	—	—	5.02 ± 1.44 (5)	*324.8 ± 9.06 (6)	35.0 ± 5.19 (8)
Apr. 1980	19.0	—	—	**15.5 ± 9.72 (4)	340.5 ± 16.09 (4)	37.8 ± 7.63 (4)
May 1980	23.0	—	—	9.22	334	35.3 ± 5.90 (4)
June 1980	24.0	—	—	2.28 ± 2.46 (6)	305.3 ± 19.1 (6)	34.3 ± 4.35 (9)
July 1980	25.0	—	—	5.73 ± 6.66 (7)	*329.4 ± 26.27 (7)	35.5 ± 6.87 (6)
Aug. 1980	28.0	—	—	6.8	327	32.9 ± 4.8 (2)
Sept. 1980	—	—	—	7.8 ± 2.61 (5)	*332.6 ± 9.81 (5)	34.3 ± 4.89 (7)
Nov. 1981	24.0	—	—	9.43 ± 4.56 (9)	*330.1 ± 19.12 (9)	35.3 ± 5.27 (9)
Feb. 1982	19.0	3.51 ± 0.27 (4)	1.17 ± 0.367 (4)	6.78 ± 2.04 (10)	309.0 ± 28.8 (10)	33.7 ± 5.85 (10)
Mar. 1982	18.0	3.42 ± 1.39 (4)	0.98 ± 0.468 (3)	5.55 ± 2.51 (10)	309 ± 9.36 (10)	36.1 ± 5.71 (10)
May 1982	27.0	3.58 ± 0.07 (3)	1.31	4.41 ± 3.8 (10)	*329.4 ± 20.3 (10)	31.8 ± 3.60
June 1982	24.5	—	—	4.45 ± 2.11 (9)	314.8 ± 10.9 (9)	34.08 ± 5.46 (6)
Aug. 1982	—	**16.2 ± 8.1 (3)	1.12 ± 0.18 (3)	6.19 ± 4.49 (9)	*343.3 ± 23.1 (9)	33.0 ± 2.68 (7)

no pattern is discernable, peaks being found in November and May (Table 1). The lowest plasma calcium for an individual was 0.19 mM and the highest 4.90 mM. For the whole population the mean is 1.53 ± 0.76 mM (n = 115).

Magnesium

The population mean is 2.10 ± 0.542 mM (n = 88). The lowest and highest values for individuals were 0.96 and 3.80 mM respectively, a smaller excursion than that found for calcium. It appears that plasma magnesium levels are under comparatively tight control.

Osmotic Pressure

The osmotic pressure values showed the greatest absolute excursion, individuals ranging from 258 to 360 mOsm. The lowest monthly means were found from January to March of each year (Table 1). The average osmotic pressure for the whole population was 321.3 ± 24.10 mOsm (n = 117).

Urea

Plama urea values showed the greatest relative range in individuals, 0.4-23.8 mM. Interestingly, the pattern of changes is remarkably similar to that of the osmotic pressure (Fig. 1), suggesting strongly that both are linked in some way. The mean value for the population (6.57 ± 5.82 mM, n = 101) is very similar to that reported for the same species (6.0 mM, Dessauer 1970).

Glucose

In the field blood glucose was remarkably steady at about 1 mM (Table 1), suggesting that blood glucose levels are highly regulated. This value is considerably lower than that reported earlier for the loggerhead sea turtle (3.3 mM, Dessauer 1970).

Lactate

For most loggerhead sea turtles the blood lactate concentrations ranged from 3 to 4 mM shortly after capture (Table 1). However, noticeably higher lactate values (8.8-16.2 mM) were obtained from sea turtles caught in a single trawl (August 1982). This was possibly the result of more severe trawl stress. Rates of recovery while on deck varied. For 6 individuals, lactate had declined an average of 16.8% from the initial value after 3 h; for 4 sea turtles after 4 h, average lactate had declined 52.6%; and for 4 sea turtles lactate had declined 16.4% after 5 h.

DISCUSSION

This study examines, for the first time, the monthly changes in the blood chemistry of a marine turtle. However it must be borne in mind that this is a field study without "controls" and alterations in body chemistry and metabolism could be due to intrinsic biological rhythms cued to extrinsic factors such as photoperiod or could be directly determined by environmental changes in, for example, temperature. As turtles are ectotherms (with the possible exception of leatherbacks) seasonal changes in temperature will be accompanied by matching changes in body temperature. It was not possible, therefore, to distinguish between temperature effects per se and changes due to annual rhythms acting as Zeitgebers. Temperature effects are the subject of a separate study (Lutz and Dunbar-Cooper 1984).

The total sample number assembled over the course of this study for each blood constituent is very large, as far as we are aware the set is much
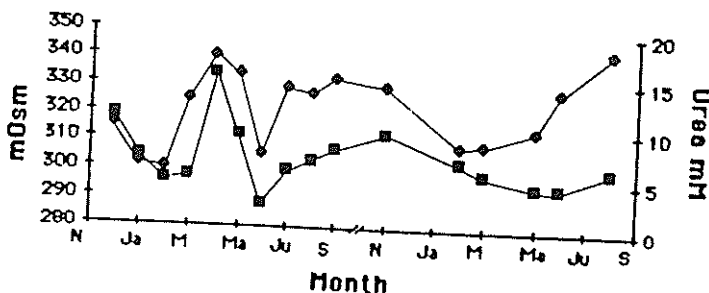

FIGURE 1.—Seasonal changes in plasma urea (■) and osmotic pressure (♦) in the loggerhead sea turtle, December 1979 to September 1981 and November 1981 to August 1982.

larger than any previous study on reptiles, and allows some general comments on the composition of sea turtle blood to be made.

The osmotic pressure found in this study, of 321 mOsm, is significantly lower than that found by Schoffeniels and Tercafs (1965) for the loggerhead sea turtle (465 mOsm), and the value 408 mOsm quoted by Dessauer (1970). It is, however, similar to that found for other reptiles including crocodiles and freshwater turtles (about 290 mOsm, Dessauer 1970). The observation, therefore, that marine turtles have relatively high osmotic pressures (Minnich 1982) would appear unwarranted. Plasma sodium and chloride concentrations are so much less than those reported for the sea snake *Pelamis platus* caught in the wild (Na = 210 mM, Cl = 167 mM, Dunson and Elhart 1971) that phylogenetic considerations may be involved. Potassium values found in this study (3.8 mM) fall within the range characteristic of other reptiles (3-6 mM, Dessauer 1970) arguing against the observation that sea turtles have peculiarly high potassium concentrations (Dessauer 1970). Magnesium values are similar to those reported for other turtles, including sea turtles (Minnich 1982) but calcium is rather low (1.5 mM this study, 3.1 mM quoted by Dessauer 1970). As mentioned above, the hematocrit, glucose, and urea data agree with earlier estimations.

The changes observed in this study are of considerably physiological significance if internal ionic concentrations are used to regulate the activity of ion sensitive metabolic pathways (Lutz 1975) particularly if some salts, such as Na, K, and Cl, have highly perturbing effects on enzyme function (Hochachka and Somero 1984).

The contrast between the behaviour of sodium and chloride is of interest. Sodium shows a wide excursion in values throughout the year with several peaks and troughs but tends to rise as the year progresses. Compared with sodium, chloride is relatively constant and the minor changes that do occur do not match in time with those of sodium. Although both ions account for most of the plasma osmotic pressure (78.5%), neither by themselves was significantly related to osmotic pressure. Changes in either sodium or chloride do not determine changes in osmotic pressure. Lance (1976) found likewise that plasma sodium showed a much wider excursion than plasma chloride in the cobra *Naja naja*, but in this species only a single summer sodium peak was seen. It is noteworthy that the lowest sodium values were found in the coldest month (February 1980, Table 1). A winter decrease in plasma sodium has been found for several freshwater turtle species, particularly those hibernating (Gilles-Baillien 1974).

We found that plasma potassium increased as the summer progressed and laboratory data suggests that this may be a temperature related phenomenon (Lutz and Dunbar-Cooper 1984). A rise in plasma potassium during the warmer months has also been observed in the lizard *Trachysaurus rugosus* and the terrapin *Malaclemys centreta* (Gilles-Baillien 1973). However, the pattern is not constant; a fall has been seen in *Varanus grisus* (Haggag et al. 1965) and no change seen in *Pseudemys scripta* (Hutton and Goodnight 1957).

Although highly variable, calcium values are low. There are several peaks per year but no consistent pattern was seen. It is very likely, however, that the changes in blood calcium reflect changes in physiology. High values have been found in some reptiles during vitellogenesis (as high as 34 mM, Lance 1976) and calcium has also been found to rise to extraordinary high levels in cold torpoid freshwater turtles (Jackson et al. 1984).

The seasonal changes in magnesium were much smaller over this study suggesting that wide excursions from this narrow range would be indicative of exceptional circumstances.

One of the most remarkable findings of this study is the parallel sweeps in the patterns shown by blood urea and osmotic pressure. As far as we are aware such a phenomenon has not been reported before. It is not simply a matter of changes in urea concentrations causing changes of osmotic pressure since the magnitude of the urea changes are much less than those of osmotic pressure. An integrated response is called for; possibly the perturbing effects of increasing osmotic pressure are compensated by heightened urea levels (Yancey et al. 1982). In loggerhead sea turtles, blood urea concentration would not appear to be diet determined since we observed that captured loggerhead sea turtles held at RSMAS, which were all fed the same food, had widely different urea values (range 3-21 mM). Interestingly, the field group with outstandingly high urea levels (April 1980) were all males.

The unchanging glucose levels demonstrate a high degree of conservatism. Seasonal changes in blood glucose have been observed in alligators with higher levels in the summer (Coulson and Hernandez 1980). In *P. scripta*, on the other hand, blood glucose increases during winter (Hutton and Goodnight 1957).

The hematocrit was also remarkable in its constancy, contrasting with other reptiles where seasonal changes in hematocrit have been recorded; typically as an increase during winter (Duguy 1970; Gilles-Baillien 1974). In contrast, the very low values

for December 1978 stand out strongly as a set by themselves and indicate some special condition.

The lactate values are of interest in that they give an index of the stress of capture in the trawl net. For quiescent loggerhead sea turtles kept in captivity at RSMAS, blood lactate is very low (0.2-0.4 mM). The initial blood lactate values obtained on deck were, by contrast, 10-80 times higher (3.2-16.2 mM, Table 1). Down to at least 3-4 mM, the rate of lactate recovery for sea turtles held on board was clearly concentration dependent (Fig. 2, $P < 0.01$). If the rate did not further decline, then it would take about 20 h for full recovery of the least stressed sea turtles in this study (those with initial blood lactate values of 3-4 mM). If the rate of decline continued to be concentration dependent then the recovery time would be much greater.

Unfortunately, since no lethargic loggerhead sea turtles were found during this study, one of its principle objectives, the identification of the state of hibernation in sea turtle, was not realizable. This occurred because South Florida has been blessed with warm winters since 1975 and water temperatures have not been lower than 15°C in the Cape Canaveral region. Nevertheless, the wealth of information on the seasonal changes in blood chemistry we now have is sufficient to enable a clear diagnosis of hibernation in sea turtles if and when animals in this condition are found. Magnesium is a prime candidate for such a purpose, since this study identifies the normal range for plasma magnesium throughout the year. Substantial increases in blood magnesium have been seen in many hibernating animals, including mammals and reptiles

(Haggag et al. 1965; Soivio and Kristoffersson 1974; Al-Badry et al. 1983). Significant changes in plasma sodium and potassium have also been associated with hibernation in reptiles (Gilles-Baillien 1974). The normal range of potassium is so narrow that extraordinarily high values should be easily detected. Substantial increases in blood lactate have been associated with cold torpor in several freshwater turtles (Jackson et al. 1984); however, as we have seen elevated blood lactate can occur with stress. And finally hematocrit is of high interest since significant changes in hematocrit, both increases and decreases, have been widely reported in hibernating reptiles (Gilles-Baillien 1974). With a single exception, hematocrit was remarkably steady over the course of this survey, and perhaps significantly, the exception occurred in the coldest month encountered. Perhaps the very low hematocrits found in December 1979 were part of a preparatory condition for hibernation.

ACKNOWLEDGMENTS

LITERATURE CITED

AL-BADRY, K. S., AND H. D. TAHA.
 1983. Hibernation-hypothermia and metabolism in hedgehogs. Changes in water and electrolytes. Comp. Biochem. Physiol. 74A:435-441.
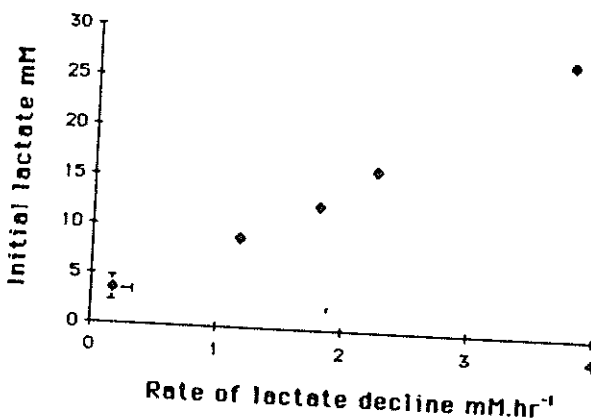

FIGURE 2.—Rate of blood lactate decline compared to initial lactate concentration for shrimp trawl trapped loggerhead sea turtles held on board ship for 3-5 h. For the lowest data point $n = 11$, SDs are illustrated. For other data points $n = 1$.

ALTMAN, P. D., AND K. C. BRACE.
    1962. Red cell life span in the turtle and toad. Am. J. Physiol. 203:1188-1190.
BENTLEY, T. B., AND A. DUNBAR-COOPER.
    1980. A blood sampling technique for sea turtles. Contract No. Na-80-GE-A-00082 for the National Marine Fisheries Service. September 1980.
CARR, A., L. OGREN, AND C. MCVEA.
    1980. Apparent hibernation by the Atlantic loggerhead turtle off Cape Canaveral, Florida. Biol. Conserv. 19:7-14.
COULSON, R. A., AND T. HERNANDEZ.
    1980. Alligator metabolism — Studies on chemical reactions *in vivo*. Permagon Press, Lond.
DESSAUER, H. C.
    1970. Blood chemistry of reptiles: physiological and evolutionary aspects. *In* C. Gans and T. S. Parsons (editors), Biology of the reptilia, p. 1-72. Morphology 3. Acad. Press, N.Y.
DUGUY, R.
    1970. Le sang des reptile. Traite de Zoologie 14:474-498.
DUNSON, W. A.
    1970. Some aspects of electrolyte and water balance in three estuarine reptiles, the diamondback terrapin, American and "salt water" crocodiles. Comp. Biochem. Physiol. 32:161-174.
DUNSON, W. A., AND G. W. ELHART.
    1971. Effects of temperature, salinity and surface water flow on distribution of the sea snake, *Pelamis*. Limnol. Oceanogr. 16:845-853.
FISHER, K. C., AND J. F. MANERY.
    1967. Water and electrolyte metabolism in heterotherms. *In* K. C. Fisher, et al. (editors), Mammalian hibernation, Vol. III, p. 235-279. American Elsevier, N.Y.
GILLES-BAILLIEN, M.
    1973. Hibernation and osmoregulation in the diamondback terrapin *Malaclemys centrata centrata* (Latreille). J. Exp. Biol. 59:45-51.
    1974. Seasonal variations in reptiles. *In* M. Florkin and B. T. Scheer (editors), Chemical zoology, Vol. IX, p. 353-376. Acad. Press, N.Y.
HAGGAG, G., K. A. RAHEEM, AND R. KAHLIL.
    1965. Hibernation in reptiles. I. Changes in blood electrolytes. Comp. Biochem. Physiol. 16:457-465.
HOCHACHKA, P. W., AND G. N. SOMERO.
    1984. Biochemical adaptation. Princeton Univ. Press, Princeton, NJ.
HUTTON, K. E., AND C. J. GOODNIGHT.
    1957. Variations in the blood chemistry of turtles under active and hibernating conditions. Physiol. Zool. 30:198-207.
JACKSON, D. C., C. V. HERBERT, AND G. R. ULTSCH.
    1984. The comparative physiology of diving in North American freshwater turtles. II. Plasma ion balance during prolonged anoxia. Physiol. Zool. 57:632-640.
LANCE, V.
    1976. Studies on the annual reproductive cycle of the female cobra, *Naja naja*. Seasonal variation in plasma inorganic ions. Comp. Biochem. Physiol. 53A:285-289.
LUTZ, P. L.
    1972. Extracellular spaces and composition of various tissues of the perch. Comp. Biochem. Physiol. 41A:187-193.
    1975. Adapative and evolutionary aspects of the ionic content of fishes. Copeia 1975:369-373.
LUTZ, P. L., AND A. DUNBAR-COOPER.
    1984. Effect of forced submergence and low seawater temperature on the physiology and behavior of sea turtles. Final report to National Marine Fisheries Service, Contract FSE 81-125-60.
MINNICH, J. E.
    1982. The use of water. *In* C. Gans (editor), Biology of the reptilia, Vol. 12, p. 325-395. Acad. Press, N.Y.
OGREN, L., AND C. MCVEA, JR.
    1982. Apparent hibernation by sea turtles in North American waters. *In* K. A. Bjorndal (editor), Biology and conservation of sea turtles. Smithson. Inst. Press Conserv., Wash. D.C., 583 p.
SCHOFFENIELS, E., AND R. R. TERCAFS.
    1965. Adaptation d'un reptile marin. *Caretta caretta* L. a l'eau douce et d'un reptile d'eau douce, *Clemmys leprosa* L. a l'eau der mer. Ann. Soc. R. Zool. Belg. 96:1-8.
SOIVIO, A., AND R. KRISTOFFERSSON.
    1974. Changes in plasma main inorganic ion concentrations during the hibernation cycle in the hedgehog (*Erinaceus europaeus* L.). Ann. Zool. Fenn. 11:131-134.
YANCEY, P. H., M. E. CLARK, S. C. HAND, R. D. BOWLUS, AND G. N. SOMERO.
    1982. Living with water stress: Evolution of osmolyte systems. Science 217:1214-1222.